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SOCIETIES OF SPIDERS COMPARED TO THE SOCIETIES OF INSECTS[1]

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ABSTRACT

Since the earliest studies of social behavior in spiders, their social structure has often been compared with that of social insects. A preliminary conclusion was that the degree of evolution of spider societies was significantly lower than that found in insects. However, we wonder if the problem has been correctly posed. In light of Wilson's and Michener's works, enriched by those of the French School (Grasse, LeMasne), we accept the definition of insect societies with all the terms which seem necessary to characterize them, namely inter-attraction and its multiple consequences, social polymorphism and dominance. In our analysis, we evoke overlap of generations and the foundation of societies to demonstrate the inherent contradiction of comparing social behavior of insects and spiders. The sociality of spiders, which actually seems to exclude the dominance and hierarchy of individuals, is paradoxically catalogued among inferior societies. With insight gained from recent studies, we suggest here that social evolution in spiders has developed along a clearly alternate track, which has rarely been followed in the animal kingdom. This type of egalitarian society is difficult to achieve in nature, and thus it is quite rare; and social spiders, whose societies are based on this principle, represent in fact very few species.

INTRODUCTION

Knowledge of social phenomena in spiders has developed considerably more recently than that in insects. It was therefore inevitable that the latter should be used as a reference point, especially as the first in-depth studies on the biology of social spiders had been carried out by entomologists who were specialists of social insects. As with insects, spiders show various levels of social evolution, from the solitary species to those which live in groups all their life. However, unlike insects, and despite the huge number of species, there are very few spiders which have passed the ultimate steps to social life. It would appear that they have followed quite a different path in their evolution, because under close examination, their sociality is noticeably different from that of insects. The social organization of insects can, to some extent, be compared to that of a number of societies of vertebrates, whereas the schemes adopted by social spiders are rarely realized in nature.

We shall not examine the whole picture of evolution of social phenomena in insects and spiders here; it would not be useful as the work has already been done by others (Shear 1970, Kullman 1972, Burgess 1976 Brach 1977, Krafft 1979,

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1982, Buskirk 1981). We shall, instead, compare the characters which are considered to define eusociality in insects, and examine how social spiders may be compared to this scheme. We shall then be in a better position to understand what is essentially original in spider societies.

SOCIETIES OF INSECTS

Wilson (1971) and Michener (1969, 1974) suggest that a "eusocial" species is defined by 1) an overlap of generations, with the mother often surviving its offspring, 2)adults taking care of the young, and 3)the presence of castes.

This general definition needs to be enriched by what has been written on this subject for a long time by other authors (for example LeMasne 1952, and Grasse 1938, 1952).

Inter-attraction in Societies of Insects and its Consequences.—The preliminary basis necessary for any social life is the inter-attraction between individuals of a conspecific group. This is certainly not particular to eusocial forms, and this is probably why Wilson (1971) does not mention it. However, in highly evolved societies, this factor is of prime importance, as inter-attraction is the *compulsory* characteristic with which all individuals have to comply. For a eusocial insect under experimental conditions, survival in isolated conditions is possible. Eusocial insects in nature, however, are never solitary, except where the individual remains isolated, but only during a transitory period, and at a very specific moment of its existence.

The fact that in evolved societies, each individual is necessarily associated with the other members of the group to which it belongs, leads consequently to an interdependence between individuals. As eusocial insects live socially all their lives, one finds in such a society, animals of all ages, and at all stages of development; this distinguishes them from the lower forms of sociality, where the individuals live in groups only at a particular stage of their life, such as the larvae of the same generation (e.g., processionary caterpillars, Balfour-Browne 1926, O'Byrne 1927). Consequently, the colony will have defined composition, and to be in equilibrium, certain standards will have to be respected. Directly linked with the structural pattern of societies and the mutual interdependence of individuals, is the observation that these societies are often close to any individuals from another colony (even conspecific).

Another important consequence of inter-attraction is the appearance of collective tasks, i.e. some members of an insect society momentarily undertaking the same task are capable of accomplishments that individuals working separately cannot achieve (Darchen 1958). About this subject, Grasse (1952) wrote: "Fortune and misfortune of social life: the group takes possession of the individuals' potentials, increases them, exalts them and makes even new ones appear; but its members lose their freedom of action and cannot subsist outside of it." In other words, the study of the isolated bee or termite is of limited value. There are, in fact, so many physiological interactions, behavior patterns and regulations among social insect groups that there can be no doubt about the integration of the characteristics of the individuals of the group. In short, social insects groups present problems that are unique to them.

From the species belonging to lower societies, to the eusocial ones, there is an increasing complexity of tasks. However, the level of complexity of tasks is not always proportionate to levels of complexity of the other features of sociality in a given species. Thus, for example, constructions of the pine processional caterpillar are far more sophisticated than the nests of some ants, although there can be no comparison between a group of these caterpillars and a society of such ants. It is, however, in the highly evolved societies that the highest sum of varied collective activities can be found. Cleaning of nests, construction, "agricultural" activities, and care of the young are all examples of behavioral development schemes requiring complex coordination between individuals. Care of the young represents in fact only one of the manifestations of sociality. This behavior can also appear in species which, from another point of view are frankly solitary (such as the forficulid *Labidura riparia*) (Vancassel 1977, Caussanel and Karlinsky 1984). Thus, the overall level of activity issuing from the inter-attraction of social insects is a more exact index of the level of sociality of the species considered, than the simple consideration of the care of the young.

The evolved society even behaves as a super-organism which has its own laws and surpasses those of the individual. Thus in the *Apis mellifera* bee, the groups of wax-making workers in charge of construction have a degree of efficiency which cannot be compared with the skill of an isolated worker who is unable to build anything (Darchen 1958, 1978). The heat produced by the metabolism of one bee is insignificant, but the whole hive maintains the temperature at around 31°C, thanks to subtle coordination between the animals which are grouped around strategic points or disperse themselves and produce ventilation according to the need to heat or cool the hive, mainly in relation to larvae. Finally, the "stigmergy" behavior (Grasse 1939, 1952) means an interaction between the result of a given act (state of construction, for instance) and the individual which perceives it; this allows an adjustment, in time and space, of behavior with regard to the task to be done, thus assuring the coordination of the operations in the group.

In evolved societies, the collective tasks and regulation systems which modulate them reach peaks of perfection, thanks to the existence of many communication systems which interact. In this respect, the ultimate level reached in the evolution of inter-attraction in eusocial insects, is the development of forms of language (tactile, chemical) essentially needed for the coordination of the group life. The society is not a simple summation of individuals, but the product of inter-action between animals, which are behaviorally linked to one another.

Social Polymorphism: Castes and Hierarchies.—Another characteristic of insect societies is social polymorphism. In some insects where a group effect is present (acridids, aphids, etc.) a certain polymorphism can be noted, but no where does it attain such an intensity as in eusocial insects. Except in a few cases (for instance some wasps), the morphology and physiology of the adult individual is determined during the larval stage. The soldier termite will never reproduce; the worker will have feeding glands, atrophied ovaries and working wax glands; the queen bee will never produce royal jelly or wax, but will be an egg laying machine, etc. Thus, the social polymorphism of eusocial insects corresponds to the existence of specialized castes. It allows for greater efficiency of individuals and constitutes one of the unique traits of this type of insect.

The existence of hierarchies is an essential characteristic of insect societies, so that two notions of hierarchy formation and evolved insect societies are fundamentally linked. These hierarchies can in fact be constitutional or acquired:

(a) Constitutional hierarchies can be found, for example, in *Apis mellifera* where the queen bee is morphologically, anatomically, physiologically and ethologically different from the worker; (b)On the contrary, the queen wasps *Polistes gallicus* the hierarchy can be acquired in time and according to the circumstances (Deleurance 1957), In effect in spring time it is not infrequent that several young queens group together to start a nest. Together, things work out better than if alone, but these colonies are normally monogynous; this is why, after some days of collaboration, dominance behavior appears among these queens, and a hierarchy is created among them. The most dominant wasp systematically devours the eggs laid by its companions and lays in their place. The other wasps eventually accept this pattern, and do not lay any more. Their physiological castration becomes real and they then take the rank of worker. Thus the castes are being established de facto before the hatching of the first eggs which will only then produce "normal" workers. It should be mentioned that in this species the implementation of such a hierarchy is possible because there is not, as with *Apis,* an anatomic gap between workers and queens.

Apart from these dominance phenomena and existence of castes, which are the rule in social insects, polyethism can also be noted, i.e., the assignment of different tasks to the same insect during its life time. The successive changes of assignments are linked not only to the age of the insects, but also to individual behavior in relation to some momentary needs of the society. The appearance of polyethyism may occur in relation to behavioral dominance, but not necessarily.

The individuals belonging to a particular caste have a certain anatomy, morphology, physiology and a behavior which distinguish them from those belonging to other castes, but among females of the same group, no fundamental genetic differences have been demonstrated. Caste determination is an induced phenomenon, although sometimes it occurs very early in life [e.g., the case of the ant *Pheidole pallidula* (Passera 1980) or the termite *Schedorhinotermes* (Renoux 1976)].

The Foundation of Insect Societies.—The insects belonging to an evolved society are socialized all their life long and the colony forms a closed system: thus the problem is how such societies can reproduce themselves.

The evolved societies essentially reproduce themselves according to two mechanisms:

(1) There may be a temporary isolation of reproductive individuals, which leave the original colony to start another one, e.g., Termites go by pairs (male and female). In the case of hymenoptera, these are fecund females (queens) who only undertaken the foundation of colonies. They do so either alone or by groups of queens, but in all cases these reproducing individuals produce the first broods of workers without the assistance of other castes.

(2) Sociotomy and multiplication may occur by splitting, which constitutes reproduction of colonies. In the case of sociotomy (called swarming in bees), a colony breeds a young queen which will be fecund. At a certain period the colony will divide into two, one section of the workers will stay with the young queen and the other with the old one. The larvae will remain either with one of the two groups, as in bees or will be shared between the two groups, as in army and driver ants. There is not in this case at any moment a solitary phase for any individual of the colony (Raignier 1972, Leroux 1982). The species which multiply by splitting, in order to increase the number of colonies, also do not have a

solitary phase. This mechanism is found in the case of primitive termites or in evolved ants of the genus *Formica.*

In termites, immature individuals may become mature when they have remained for too long without any contact with the royal, couple. Apart from the soldiers, which cease molting, and the white soldiers and nymphs, which are very close to their imago molt, most of the individuals of these colonies retain the potential of molting and having neotenic generation, even if they temporarily serve the function of workers. The castes in primitive termites are thus relatively dynamic and reproduction by splitting is long. In ants, the colonies which multiply by splitting are to be found in the species with polygynous colonies; these recruit queens through swarming processes. These queens can either come from the mother colony or from neighboring colonies swarming at the same time.

When a colony of ants becomes too large, a group of individuals emigrate further away. They first establish a camp of workers. This camp can organize and recruit larvae and queens. Then a satellite colony is installed, and retains contact, with the mother colony. Then after a period, one obtains either a group of independent colonies which are genetically related or a super colony composed of a certain number of satellite colonies. There is therefore no general and single system for the foundation of colonies in social insects. Ants may be those which show the greatest diversity in the modes of foundation.

One of the factors of sociality in insects which has been observed for a long time is of course the overlap of generations. The mother must survive its descendants and keep close links with them so that the society can survive. It is indispensable that the reproductive individuals (at least) have a sufficiently long life. In monogynous colonies, the life span of a colony is related to that of the queen, as occurs in some species of ants and bees. A possibility of control exists, however; in case of urgent need a colony can prepare a new queen (in *Apis* this possibility is well known) but this system remains fragile (for example the number of colonies of *Leptothorax* ants found without a queen is not negligible); such colonies are destined to extinction (Plateaux 1970, Poussardin 1984). Eusocial insects have therefore developed ways to solve this situation, and polygyny is one of them. For example, the large colonies of *Formica,* the nests of wasps *Polybia* and *Nectarina* are in principle immortal, their longevity is considerably greater than that of any individual (for example the wasp nests of *Synoeca cyanea,* 60 years (Evans and West-Eberhard 1970). The overlap of generations in such species reaches its peak and the longevity of the reproducing individuals does not affect the chances of survival of the society.

As we have seen, the three definitions proposed by Wilson to characterize a society of invertebrates clearly are too simplified, and need to be enriched by new ones.

SOCIETIES OF SPIDERS

Inter-attraction in Spider Societies.—The first study defining features of sociality in spiders was that of Kullman (1972). It was thus nearly contemporaneous with the book of Wilson (the Insect Societies, 1971). For the German author there are three real characteristics of social life in spiders: (1) tolerance, (2) inter-attraction, and (3) cooperation. There is nothing to say against this definition, but it was certainly not established using the same criteria as those given with insect societies in mind.

First, we can note that inter-attraction, which for Kullman (1972) is a pertinent characteristic, was not mentioned by Wilson (1971), as this is probably implicit for him. Yet we have seen that in insects various very important corollaries arise from the idea of inter-attraction. As in insects, inter-attraction arises sometimes in spiders whether or not they are completely social. But in the most social species it means a compulsory link which unites the members of the group. Usually no individuals live alone except for some females who are about to lay eggs and leave the nest to start a new colony.

The fact that the isolated individual of social spiders is unknown in nature poses, of course, the problem of the type of links which unite the animals among themselves. In contrast with insects, each spider is theoretically able to satisfy its needs alone. It can hunt, spin its web, lay eggs and thus survive outside this society. Naturally, one is inclined to think that inter-attraction is linked to the continuation of aggregative behavior of the young, and is essentially based on the olfactory sense. Nevertheless, it would be very interesting to have more detailed information on this phenomenon.

In this respect, it would be very instructive to make a comparative study on the physiology and behavior of two very close species, e.g., *Achaearanea disparata* (Denis) and *Achaearanea tessellata* (Keyserling). The first species is strictly found in the Gabonese forests and is at this time unknown anywhere else in the world. This is a social spider from all viewpoints and spends its entire life in a group; it spins its web and hunts in association with its companions, and forms spectacular colonies very high in the trees. *Achaearanea tessellata* is also a tropical species, but very widespread on all continents. Curiously, these two species are virtually morphologically identical. However, from an ethological viewpoint there is no possible doubt as to the fact that *Achaearanea tessellata* is solitary. What has thus happened during the evolution of the common stock of these two spiders so that they now form two different species which are, at the same time, so close and so different? A comparative study on this subject is certainly desirable.

In the spider societies of all species that have been studied, there are no closed social groups. It is possible to add to a given society individuals of any age of the same species but coming from very different locations without causing any fights. The tolerance which can be noted here, is thus one of the essential characteristics of this type of social structure. Spiders recognize their own species but show no restriction at the level of the social group. In accordance with the "non-closing" of societies, the importance of the social groups might theoretically be unlimited. However, in spiders, as in insects, each species has its standards and the population does not increase indefinitely as, beyond a certain threshold, there is a splitting of societies.

Overlap of generations is also in this instance indispensable for the survival of the society. However, in *Mallos gregalis* (Simon) there are seasonal variations in the age structure of the population of the society diminishes. In other species, as in *Anelosimus studiosus* (Hentz), the societies disperse after some months and all adult individuals separate to go here and there and initiate new families. It is clear that the cyclic diminution of the number of larvae is also known in social insects. It seems that the authors who have studied the social spiders with a short cycle have some reluctance in conceding them a social status which in fact is not refused for similar insects.

As with insects, we also find in social spiders a number of collective tasks which make these groups real entities which are very different from a summation of individuals living on their own. These collective tasks, which are called "cooperation" by Kullman are one of the corollaries of the fundamental phenomenon of inter-attraction. They concern the care of the nest (cleaning, construction, repairs), hunting, care of the eggs and cocoons (Witt, Scarboro and Peakall 1978). The analysis of collective tasks is relatively disappointing because each animal often seems to work on its own and independently of the others; however, cooperation in hunting activities has been well identified in *Achaearanea disparata* for example, and building activities in *Mallos gregalis*. From an overall viewpoint, "community behavior" is clearly present among the social spiders, and the detail of the individual movements in spiders does not differ very much from what has been observed in various insects.

In social spiders inter-attraction is accompanied, as in insects, by forms of communication, and this communication is the crucial issue. The communication system is spiders is largely based on pheromones and vibrations (Darchen 1965, 1975, Krafft 1982). The web plays an important role in the transmission of "language" as it constitutes a substratum for the smells, is a vibratory system which carries sorts of coded information. The mode of perception in spiders is probably too remote from ours for us to understand the real role a web holds for the animal that builds it and spends its life on it. If this mode of perception and communication is fundamental in spiders which make webs, it can also be found in wasps, for example *Rhopalidia cincta* where cardboard construction can also, in a way, be used as a vehicle for vibratory information for coordinating the activity of the different members of the society at a given time. The needs of the community, inherent in any social life, have thus found ways of expressing themselves (both in insects and spiders) which are essentially based on tactile auditory and odoriferous perceptions.

The existence of this "language" is perhaps what makes the essential difference between *A disparata* and *A. tessellata*. It is impossible to ignore the importance of communication in the establishment of social life, and it is a pity that Wilson has completely neglected it.

Absence of Castes in Social Spiders.—Although the presence of castes in social insects is a fundamental characteristic of eusociality, any attempt to find them in social spiders have remained unfruitful: no worker castes, no reproductive castes, and nothing which resembles classical structures of insect societies can be found in spiders.

Curiously, insect societies with more structure and hierarchy are regarded as highly derived. In contrast, those societies where the relationships between individuals fluctuate more will be catalogued as less derived, and the same happens with spider societies.

The concept of eusociality (which goes along with that of hierarchy, where the individual loses its autonomy to live in the group) obviously has a valorizing connotation whereas the social forms which have not reached the top level of hierarchy development are, we must admit, given a pejorative judgement. This is certainly why spiders have never been granted the status of advanced or derived societies; they could deserve this qualification which might in fact be of another order.

Thus, we humans show (but without confessing it, because this is probably done unconsciously) some admiration of the more hierarchical forms of society which are of an absolute monarchy type—and a much lower attraction for the forms without castes of a democratic type. However, in most modern human societies nobody would dare to give such a judgement. This finding is surprising and it shows that research even in "pure" biology sometimes leads to types of conclusions which are unconsciously biased by some cultural prejudices, and nobody in fact notices them because these prejudices are more or less the same for all.

In social spiders the tolerance pointed out by Kullman is of great importance. We have seen that it can exist vis-a-vis conspecifics coming from other colonies. We still find this tolerance in another form in these societies: first, the males are neither excluded nor attacked; and second good relations exist between females, each one having the opportunity to lay eggs and achieve the various tasks of the society. But besides this tolerance, which is the fundamental rule, it should be interesting to study the polyethism with marked animals, as research in this field is sorely lacking. The data we have on *Mallos gregalis* for example show how this field of research is interesting. This would allow us to have a more precise idea of the succession of tasks carried out by the different individuals. It is difficult to discuss in the absence of experiments, and it is only when we are in possession of precise ethograms that we can assess the degree of cohesion which links the members of a group in the various species of social spiders.

Foundation of Spider Societies.—As for insects, it is important to know how a spider society starts as this is a source of information on the nature of this society. Here again we have relatively few reliable observations (Darchen 1965, 1976, 1978, 1979, Kullman 1968, Wickler 1973, Jacson and Joseph 1973, Fowler and Levi 1980, Lubin 1981, Vollrath 1982). A spider society may start either through individuals, or through small groups of individuals who leave to make a colony nearby, or through groups of mature and immature animals which emigrate some distance from their original society.

In *Agelena consociata* individual separations have never been discovered, but the two other types of splitting are known. The individuals which leave separately are either gravid females or immature animals (*Stegodyphus sarasinorum* Karsch, Grasse and Joseph, 1973). *Anelosimus eximius* also shows solitary foundation, but not exclusively. Vollrath (pers. comm.) who has also studied the solitary foundation of societies of the latter species notes that isolated females have very few chances of survival but their chances are improved if several females join forces. We have then a type of foundation which is comparable to the polygynous type practiced by *Polistes gallicus*; in *Anelosimus eximius*, however, Vollrath does not indicate dominance of behavior among groups of females. Here again this great difference between the social systems of insects and spiders can be found, which makes the close comparisons a bit difficult.

In studying the foundation of societies, overlap of generations and the longevity or reproductive individuals are important factors to be taken into consideration. Spider species establishing large colonies have freed themselves from the constraint of individual longevity, somewhat like the social insects such as ants of the genera *Formica* or *Polyergus*. For example, Vollrath mentions a complex of colonies of *Anelosimus eximius* which is at least 14 years old, and we have seen one *Agelena consociata* colony which we have observed for 10 years. Spiders reach this result without the existence of castes.

Table 1.—Summary comparison of characteristics of insect and spider societies.

Characters	Societies of Insects	Societies of Spiders
Inter-Attraction	Obligatory. In nature, an isolated insect (excepted during a transitory period of time) does not exist, nor can it survive a long time.	Obligatory. In nature an isolated spider (excepted during a transitory period of time), does not exist. However, an experimentally isolated individual is able to survive a long time.
Stability of Societies	Equilibrium preserved by numerous internal controls.	No data.
Closure of Societies	Antagonism towards newcomers from other conspecific societies.	Tolerance. Societies open to conspecific newcomers.
Castes and Social links	Hierarchical origin of castes. Psychological castration (Dominance).	No psychological castration. All the adults are fecund. Apparent equality of all members.
Origin of Castes	Trophic origin of castes.	No castes.
Communications	Chemical (pheromones), mechanical (tactile).	Chemical (pheromones), mechanical (vibratory, tactile).
Collective Works	Complex coordination of tasks.	Complex coordination of tasks.
Polyethism	Present, linked to the physiological evolution of the individuals.	Possible, but not enough data.
Foundation of Societies	Various types of foundation -Isolation of reproductive individuals -no isolation of reproductive individuals -sociotomy -splitting Possible splitting: neotonic workers in the primitive societies of Termites, polygyny of some ants societies and wasps ones.	Scarce data. These 2 types of foundations exist, but the most successful one is realised through splittings. The splitting of the colonies are easy because all the spiders are reproducers.
Overlap of Generations	Yes, with some corollaries like brood care and nest defense.	Yes, with some corollaries like care and nest defense.
Cycle of societies	Annual and perennial.	Annual and perennial.
A "Super-Organism"?	The society is a super-organism with its own "laws" transcending the ones of isolated individuals.	Unclear due to the absence of hierarchies. However, spider societies are certainly greater than the sum of the individuals of the colony. Data are lacking.

The longevity of the founding mother is often proposed as a factor of the social life in spiders. There would be in fact a certain conflict between the overlap of generations which is indispensable to the appearance of the social life, and the death of the mother following the feeding of larvae. In this respect, social behaviors that provide individuals to take care of the brood, lead to economy in the life of the laying mothers. Then it is possible to say that social life induces the longevity of females and not the opposite (that longevity is a prerequisite to social life). This is, of course speculation, but the present behavior where the mother takes care of the young and dies soon after may be considered as a stage of the evolution of spiders towards sociality.

CONCLUSION

Tolerance, lack of caste and hierarchy, which appear among social spiders, cannot be attributed to a lower range of sociality than that of the eusocial insects, but rather, as we have tried to demonstrate, to a different kind of sociality.

A question comes to mind when considering social spiders: why has this type of society not been more successful in nature? Why are there so few social species despite the fact that they can be found in various families?

The studies which have already been carried out on these animals come to the conclusion that among the advantages of spider sociality there is: (1) an economy in the number of eggs laid; (2) better success of the hatching; (3) no repression of female reproductive capability.

We may ask ourselves again why they did not conquer more of the world, as they do not show aggression between different social groups within the species, and thus have greater chances to co-exist. One could probably reply that there are other constraints, such as difficulty for the societies to disperse over long distances (cf., Vollrath 1982), and many other arguments which could be considered in this respect.

Finally, it is certain that these spider societies are unique, given the mechanisms of tolerance they have developed and which can be contrasted to the dominance which generates castes in social insects (Table 1). It must be, that even in invertebrates, democracy is a difficult goal to achieve.

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